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Abstract

Invasive alien species (IAS) are the subset of naturalized species that cause greater impacts on biodiversity, ecosystem functions and services. However, despite management actions and eradication plans, their expansion worldwide is seemingly unstoppable. In this paper, based on a large dataset of 1039 records of IAS and native plant species representative of the extensive biogeographic diversity in Southern Europe, we tested the consistency of Grime' concept of CSR universal adaptive strategies (competitors, stress-tolerators and ruderals) to explain plant invasion across a broad elevation gradient. Accounting for phylogenetic relatedness, we tested two hypotheses. First, whether IAS occupy a different CSR space compared to native species. Second, whether the success of IAS at the regional scale is linked to higher degree of C- and/or R-selection, according to recent worldwide observations on naturalization success of alien species. We tested such hypotheses on different growth forms (trees, shrubs, short-lived herbs, long-lived herbs, hydrophytes) that are related to plant functional traits. Except for trees, IAS and native plant species essentially occupied the same CSR space, indicating that IAS can occupy the same niches of native species. However, IAS exhibited mainly higher C- scores compared to natives, indicating that IAS are more competitive and are associated with relatively productive habitats, involving that these sites are highly prone to invasion (and that native species in resource-poor habitats are less likely to experience pressure from IAS). Our findings confirm the utility of CSR classification to broadly represent, and explain, the invasion success of alien plant species at the regional scale. This approach emerges as a viable tool in assessment of IAS characteristics and for development of strategies and plans for their containment.

Keywords	Competition; exotic; invasion; plant functional types; plant strategies; universal adaptive strategy theory
Taxonomy	Functional Plant Ecology, Invasive Plants, Plant Competition, Vegetation Ecology

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March 01, 2019

Dear Editors and Members of the Editorial Board,

We are pleased to submit an original research article for consideration by the "*Special issue on Plant invasions: mechanisms, impacts and management"* in *Flora.*
In this paper, we propose a regional scale analysis of Grime's CSR strategies of invasive alien plant species compared to natives. We believe that this manuscript is appropriate for publication by *this special issue* since it deals with the characteristics of invasive alien plant species and mechanisms underlying their invasiveness, which are among the main topics of biological invasion.
We hope you will find the manuscript interesting and relevant for publication by *this special issue* in *Flora*.

Sincerely,

Michele Dalle Fratte (on behalf of all Authors)

Highlights

- Grime's CSR strategy theory broadly explain the invasion success of alien plant species
- Invasive alien and native plant species occupy the same region within the CSR space
- Invasive alien plant species are true competitors
- CSR theory can be a viable tool for the risk assessment of invasive alien plant species

Alien plant species invade by occupying similar functional spaces to native species

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Abstract

Invasive alien species (IAS) are the subset of naturalized species that cause greater impacts on biodiversity, ecosystem functions and services. However, despite management actions and eradication plans, their expansion worldwide is seemingly unstoppable.

In this paper, based on a large dataset of 1039 records of IAS and native plant species representative of the extensive biogeographic diversity in Southern Europe, we tested the consistency of Grime' concept of CSR universal adaptive strategies (competitors, stress-tolerators and ruderals) to explain plant invasion across a broad elevation gradient. Accounting for phylogenetic relatedness, we tested two hypotheses. First, whether IAS occupy a different CSR space compared to native species. Second, whether the success of IAS at the regional scale is linked to higher degree of C- and/or R-selection, according to recent worldwide observations on naturalization success of alien species. We tested such hypotheses on different growth forms (trees, shrubs, short-lived herbs, long-lived herbs, hydrophytes) that are related to plant functional traits.

Except for trees, IAS and native plant species essentially occupied the same CSR space, indicating that IAS can occupy the same niches of native species. However, IAS exhibited mainly higher C-scores compared to natives, indicating that IAS are more competitive and are associated with relatively productive habitats, involving that these sites are highly prone to invasion (and that native species in resource-poor habitats are less likely to experience pressure from IAS). Our findings confirm the utility of CSR classification to broadly represent, and explain, the invasion success of alien plant species at the regional scale. This approach emerges as a viable tool in assessment of IAS characteristics and for development of strategies and plans for their containment.

Key words

Competition; exotic; invasion; plant functional types; plant strategies; universal adaptive strategy theory

Introduction

Species introduction outside their natural boundaries is a rapidly increasing phenomenon fostered by globalization processes (Meyerson & Mooney, 2007; Guo et al., 2019). Despite the lack of problems caused by many of these species on introduction to new locations, some become invasive (invasive alien species, IAS) and represent one of the major anthropogenic threats to ecosystem integrity worldwide, with impacts on biodiversity, ecosystem functioning and services (Pejchar & Mooney, 2009; Vilà et al., 2011). In Europe, which has a long history of species introduction (Lambdon et al., 2008b), risk assessments, early detection and eradication plans, and management actions have been widely implemented (e.g. Regulation No 1143/2014 of the European Parliament). Nevertheless, the expansion rate of IAS continues to increase (Pyšek et al., 2017), damaging economic and social aspects of human well-being. Thus, understanding the ecological characteristics of IAS could provide supporting information to develop more effective measures for their containment.

Among plant species, IAS are recognised as those that rapidly broaden their spatial distribution by expanding into existing native plant communities (Richardson et al., 2000). Although invasions start from natural or human induced dispersal processes, a range of biological and physical factors can provide the opportunity for IAS to rapidly outcompete native species (Rejmánek et al., 2005a). The success of IAS is often attributed to their capacity for rapid growth through high resource acquisition, particularly in non-resource limited conditions (Pyšek & Richardson, 2008; Funk, 2013). However, Leishman et al. (2010) showed that IAS and native species do not have fundamentally different carbon capture strategies, supporting the concept of community invasibility, i.e. characteristics of the resident communities favouring invasion (Richardson & Pyšek, 2006). Specifically, according to trait-environment relationships (Dalle Fratte et al., 2018), differences between IAS and native plant species can reflect environmental conditions of the sites where they occur rather than differences between species *per se* (Leishman et al., 2010).

Pyšek & Richardson (2008) reviewed the literature in an attempt to identify the traits characteristic of invasive vascular plant species, finding evidence only for some traits that are universally associated with these species: height, vigorous vegetative growth, early and extended flowering. Van Kleunen et al. (2010) demonstrated that IAS tend to outcompete native or non-invasive species due to higher values of functional traits related to growth rate and resource acquisition. Also consistent with a 'soft leaves, fast growth' strategy, the most successful alien species are those that minimize carbon investment in leaf construction, as observed both in terrestrial (Tordoni et al., 2019) and aquatic vascular flora (Lukács et al., 2017). Nevertheless, the debate concerning native vs. alien suites of traits is ongoing since patterns or common features are not always clear (Hulme & Bernard-Verdier, 2018; Funk et al., 2017). Daehler (2003) suggested that there is no unique set of traits responsible for invasiveness, but that multiple suites of traits could explain invasion success in different environments (e.g. Tecco et al., 2010; Funk et al., 2016).

Multiple adaptive traits can be summarized in terms of the ecological strategies or the group of functional traits involved in plant resource economics (determining matter and energy turnover rates) and size (denoting the absolute amount of matter and energy present within organisms and within biotic communities) (Díaz et al., 2016; Pierce et al., 2017). Grime's CSR life-strategy theory provides a conceptual framework to classify species into competitive (C), stress-tolerant (S) and ruderal (R) strategies (Grime & Pierce, 2012), and is currently the only plant strategy theory that agrees with resource economics and size as the principal axes of adaptive variation, and can place these in the

context of environmental selection pressures (Pierce & Cerabolini, 2018). There are a range of advantages in using adaptive strategy theory, rather than single traits, to evaluate the interactions among alien and native species (Davis, 2009; Rejmánek et al., 2005b; Guo et al., 2018; 2019) and the effects on ecosystem services provision due to plant invasion (Vicente et al., 2013). The application of CSR strategy theory to studies at a local to regional-scale, has highlighted that amongst alien plant species, R- and C- selected species and their intermediate strategies (CR) are prevalent, while S-selected species are under-represented (Pyšek et al., 2003; Lambdon et al., 2008a; Dainese & Bragazza 2012; Alexander et al., 2016). Despite this pattern also being evident at the global scale (Guo et al., 2018; 2019), Hulme et al. (2018) raised some questions concerning the use of CSR theory to categorize alien species, since it may mask individual trait differences. Indeed, though CSR strategies can potentially provide a robust theoretical context to predict the performance of species in a definite environment (Grime & Pierce, 2012), it is necessary to experimentally validate the potential for CSR strategy theory to discriminate IAS and to predict their capacity to invade.

In this study, we used a large regional flora dataset based on IAS and native species characteristic of Southern European vegetation to test two hypotheses. First, we tested whether IAS and native plant species occupy the same or a different space within the ternary combination imposed by CSR strategies; hence, contrary to the habitat invasibility concept (Leishman et al., 2010), the capacity to invade depends on differences in carbon accumulation strategies. A secondary hypothesis was that at the regional scale the invasion success of alien species is linked to a higher degree of C- and R-selection, according to recent global findings of naturalization success of alien species (Guo et al., 2018). We tested these hypotheses for different growth forms (trees, shrubs, short-lived herbs, long-lived herbs, hydrophytes) using plant functional traits common across growth forms (Pierce et al., 2017).

Methods

Study area

The study area was the Lombardy administrative region of Italy, which covers an area of 23,870 km^2 ranging between latitudes 44°40' − 46°37' N, from the Apennines to the Alps, and longitudes 8°29' − 11°25' E, from Lake Maggiore to Lake Garda. The elevation spans 10 meters a.s.l. in the Po Valley to approximately 4,000 meters a.s.l. on Mount Bernina. The study area includes both the Alpine and Continental biogeographical regions (ETC/BD, 2006), and spans from continental to oceanic bioclimates (Pesaresi et al., 2014), although it is characterized by a highly variable mesoclimate due to its complex orography. Geological substrates consist of a wide range of litho-types, both silicate or carbonate rocks, alluvial or morainic deposits. This extensive environmental variability is consistent with the heterogeneity of vegetation communities, ranging from Mediterranean holly oak woods near Lake Garda to Alpine tundra in the highest mountain regions.

Dataset

The dataset included all records of plant functional traits for the species analysed by Dalle Fratte et al. (2018), to which we added some unpublished data. Many records are available from Authors' datasets in TRY (Kattge et al., 2011; https://www.try-db.org/: see datasets n. 227, 228, 229, 371, 372 and related references).

IAS are defined as naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: > 100 m / < 50 years for taxa spreading by seeds and other propagules; > 6 m / 3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area (Richardson et al., 2000). We established the status of native or invasive species in Lombardy according to literature (Assini et al., 2010; Galasso et al., 2018).

A rapid decrease in alien species richness with increase in elevation was detected in adjacent regions of Italy (Barni et al., 2012) and more generally in the European Alps (Becker et al., 2005). The upper montane belt was considered the highest elevation attained by alien species, beyond which they were rarely observed. Given the high elevation gradient of the study area, species exclusively growing in subalpine or alpine belts, i.e. with the ecological index of T (temperature) from 1 to 2.5 according to Landolt et al. (2010), were removed from the dataset. In the analysis, we also considered species listed as "x" for T index (Landolt et al., 2010), since they can spread along a wide portion of the elevation gradient.

The final dataset thus consisted of 1039 records, including 59 tree species, 94 shrubs, 224 short-lived herbs (annual or biennial graminoids and forbs), 601 long-lived herbs (perennial graminoids and forbs) and 61 hydrophytes (Table 1). We assigned each species to the growth forms identified by Guo et al. (2018): trees, shrubs, short-lived herbs, and long-lived herbs, but considered hydrophytes separately, given their specific ecological constraints. Finally, we computed the C-, S-, and R- scores for each species according to the *StrateFy* tool of Pierce et al. (2017).

Phylogenetic tree

We built a phylogenetic tree of the species in our dataset using the *PhytoPhylo* megaphylogeny tree implemented by Qian & Jin (2016). Following their recommendations, we used their 'Scenario 1' to solve the phylogeny at the species level in our dataset. This scenario is the most cautious, as it

adds genera or species as basal polytomies within their families or genera to avoid random solutions. Before processing the phylogenetic tree, names of every taxon (family, genus and species) in our dataset were standardized according to The Plant List (www.theplantlist.org) using the R package '*Taxonstand*' (Cayuela et al., 2017).

Statistical analysis

The CSR classification indicates proportion for each element (C, S and R) along each axis, and thus represents an integrated trade-off between traits, i.e. the three axes are dependent on each other (Pierce et al., 2017). We used the R package '*compositions*' (van den Boogaart et al., 2018) to visualize the ternary diagrams of the CSR strategies of IAS and native species. To account for the compositional structure of the data (van den Boogaart & Tolosana-Delgado, 2013) we first transformed the dataset of CSR scores with Isometric Log-Ratio Transformation (ilr), which reduced the ternary dataset to a two dimensional image. To test the first hypothesis, i.e. whether invasive and native plant species occupy different CSR space, we computed phylogenetic multivariate analysis of variance (MANOVA) to compare native vs. invasive alien species inside the distribution provided by the ternary combination of CSR scores. In addition, to check for the second hypothesis, i.e. whether the invasion success of alien species is correlated with a higher degree of C- and R- selection, we computed a phylogenetic univariate analysis of variance (ANOVA) considering each axis (C-, S-, and R-) as independent. Before running the ANOVA, we checked for normality of C-, S- and R-scores by means of Shapiro-Wilk normality test, according to which it was not necessary to transform the variables. We computed both phylogenetic MANOVA and ANOVA by means of the function 'aov.phylo' in the R package '*Geiger*' (Harmon et al., 2007), which accounts for the phylogenetic tree produced by the '*S.PhyloMaker*' R function (Qian & Jin, 2016). We used the R package 'ggplot2' (Wickham, 2016) to visualize the boxplots of the C-, S- and R-scores of IAS and native species. We ran both the analysis considering all the species together, as well as splitting the dataset according to the growth forms. We performed all the analysis with the software R 3.4.4 (R Core Team, 2018).

Results

In the CSR ternary space and accounting for the phylogeny (Fig. 1 and Table 2), IAS did not show any significant divergence from native species regardless of the growth form. Considering growth forms, IAS were significantly different from native species only within trees ($p = 0.02$). Invasive alien trees showed higher C- and lower S- compared to natives, but similar R- mean values (CSR compositional mean ± SD: 51.2 (C) : 38.0 (S) : 10.8 (R) ± 24.7% vs 40.2 (C) : 46.3 (S) : 13.5 (R) ± 22.5%) (Appendix A). All gymnosperm trees were classified as stress tolerant, indeed, they were clustered in the S corner of the CSR triangle; however, this did not affect the results since in our dataset gymnosperm trees were balanced between IAS and native species. Shrubs, long-lived herbs, short-lived herbs and hydrophytes did not differ between IAS and native species.

Analysing axes of CSR as independent variables and considering the phylogenetic signal (Fig. 2 and Table 3), at all species level we found higher C- scores for IAS compared to natives (mean ± SD: 36.3 ± 22.6% vs 29.8 ± 21.4%), without significant differences between S- and R- scores. Trees showed the same pattern, with IAS showing higher C- scores (44.5 ± 19.4% vs 34.6 ± 13.7%) (Appendix B). Also invasive alien shrub species showed a marked increase of C-scores compared to native species (43.5 ± 13.8% vs 23.9 ± 17.0%), but they showed significantly lower S- scores too (35.9 ± 18.0% vs 54.8 ± 26.0%). Among herbaceous growth forms, invasive short-lived herbs had higher C- scores than native species (35.5 ± 21.5% vs 26.3 ± 22.8%), while S- and R- scores did not show significant differences. Among long-lived herbs and hydrophytes, invasive alien species did not show significant differences from natives along each CSR axis.

Discussion

Our results, based on a large regional dataset of plant species characterizing the vegetation of contrasting biogeographic situations of Southern Europe, underline the relevance of CSR strategy theory (Grime & Pierce, 2012) to assess the invasiveness ability of IAS. We can confirm that there are clear patterns of CSR strategies at the regional scale (Pyšek et al., 2003; Lambdon et al., 2008a; Dainese & Bragazza, 2012; Alexander et al., 2016), which confirm and emphasize recent observation at the global scale concerning species naturalization incidence and extent based similar approach (Guo et al., 2018). Nevertheless, we observed some different responses among growth forms and with regard to the CSR space.

Our first hypothesis was that IAS and native plant species occupy a different region of CSR space. We detected clear differences only for trees, while robust patterns were not evident when all growth forms were considered together, or separately, for non-tree growth forms (Fig. 1 and Table 2). In other words, except for trees, the space occupied by IAS and native species in the CSR classification was practically identical. This finding suggests that IAS occupy a similar strategic position to native species and that other factors operate in concert with carbon accumulation strategies to drive the local success of invasion (Funk et al., 2017). For example, these factors could be linked to the phylogenetic similarity of alien and native species, which involves that IAS prefer to occupy existing phylogenetic space in native communities (Ordonez, 2014; Loiola et al., 2018). Furthermore, native communities can determine the entry of IAS depending by intrinsic habitat properties such as habitat filtering (Carboni et al., 2015) and invasibility (Leishman et al., 2010; Richardson & Pyšek, 2006; Rejmánek et al., 2005b), or to biogeographical context (Pyšek & Richardson, 2006). Hence, with the exception of trees, when different environmental gaps are available for colonization within a plant community, IAS and native species should have the same probability to colonize them. Such findings are consistent with difficulties encountered in the management of IAS, as they respond to multiple components of global change (Bradley et al., 2010) and do not differ solely with regard to plant functional types or strategies.

The second hypothesis was that the invasion success of IAS at the regional scale is associated with a high degree of C- and R- selection strategies, according to recent global findings of naturalization success of alien species (Guo et al., 2018). Analysing each axis of CSR as independent variables, we found broad evidence in support of the hypothesis that IAS tend to be competitors (Fig. 2). Efficient competitors for available resources are likely to be the best invaders in natural and semi-natural ecosystems (Pyšek et al., 1995; Rejmánek et al., 2005a). This pattern is significant when considering all species together, as well as among trees, shrubs and short-lived herbs, but not among long-lived herbs and aquatic species. Competitors are characterized by traits that enhance photosynthetic rate and rapid growth, larger leaves, high flowering frequency and nutrient rich leaves (Wright et al., 2004; Reich, 2014) and some of them (the most competitive) have been associated also to a high efficiency of clonality (Song et al., 2013). All these traits have been frequently linked with invasive plant species (Pysek & Richardson, 2008; van Kleunen et al., 2010; Roioloa et al., 2016). While very few alien species are able to invade plant communities at advanced successional stages (Rejmánek et al., 2005a), IAS tend to accumulate in early successional stages (Crawley et al., 1996), i.e. following disturbance or as part of secondary succession. In particular, early succession on fertile substrates typically promotes dominance of high-resource demanding species (Grime, 2006). Indeed, high-resource ecosystems tend to accumulate more exotic species than low-resource ecosystems (e.g. Huenneke et al., 1990; Gross et al., 2005; Stohlgren et al., 2008). After that IAS are released into new

environments, usually because they naturalize from cultivated gardens (Guo et al. 2019), such sites may be the gateway through which alien species invade a target region (Crawley et al, 1996; Rejmánek & Richardson, 1996; Pyšek et al., 2017),

Despite the fact that Guo et al. (2018) found a positive relation of R- selection with the incidence of naturalization worldwide, we did not find such evidence for IAS at the regional scale in our study system. It is possible that such differences are caused by the more specific subset of species that we used compared to the global dataset. Indeed, our analysis might be considered a specific focus of part of the study by Guo et al. (2018), as IAS are the subset of naturalized species already having extensive impact on the structure of communities and ecosystems (Pejchar & Mooney, 2009). Moreover, focusing on IAS we removed the naturalized species from our analyses, which constitutes a large proportion of the local flora (e.g., Galasso et al., 2018) that is more likely to contain a high degree of ruderals. Often such invasions start from disturbed sites (Crawley et al, 1996; Richardson et al., 2000; Pyšek et al., 2017), where species with a ruderal life strategy thrive (Rejmánek & Richardson, 1996). Hence, IAS act on ecosystem that are already modified, characterized by a lower disturbance. Furthermore, a global analysis such as that of Guo et al. (2018) represents a greater range of very specialized environments. For example, they highlighted that the high R- degree of shrubs and long-lived herbs was due to the presence of Mediterranean species, which are absent in our local flora. In addition, Guo et al. (2018) studied the naturalization capacity of species worldwide, and it is possible that some of the species we classified as native in our geographic region are classified as naturalized elsewhere in the world.

With regard to the degree of S- selection we did not find differences either within or between growth forms. Only invasive alien shrubs displayed significant lower values of S-scores compared to natives, confirming that species with a greater S-score are less likely to become naturalized (Pyšek et al., 2003; Alexander et al., 2016). Usually stress-tolerators are very long-lived, have a long leaf life-span, grow slowly, fruit later and produce fewer seeds with respect to competitors and ruderals (Grime, 1979; Grime & Pierce, 2012). All of these traits contrast with those commonly reported to be associated with successful invaders (Pyšek & Richardson, 2008; van Kleunen et al., 2010), and could make stress-tolerators less likely to be selected by humans as horticultural or gardening plants (van Kleunen et al., 2018; Guo et al., 2019). In general, stress-tolerant plants rely heavily on vegetative rather than sexual reproduction and rarely show extensive morphological plasticity, which limits their potential to spread (Grime, 1979; 1988). In addition, the chance of a stress-tolerant plant to be introduced into an environment with a stress regime comparable to the one it is adapted to in its native range is relatively low, given that stressful environments are relatively rare in general, and often characterised by idiosyncratic and restricted environmental regimes (Alexander et al., 2011; Funk, 2013). Native species appear to have a competitive advantage over IAS in low-resource ecosystems (Alpert et al., 2000; Daehler, 2003), and communities become more susceptible to invasion when resource availability is increased (Davis et al., 2000; Funk, 2013).

According to Grime (2001), woody species occupy the S-C region of the CSR triangle, while trees with high R-scores do not exist (Pierce et al., 2013; 2017). In the S- corner we found a cluster of gymnosperm tree species, while broad leaved trees were classified towards higher C (see also Pierce et al., 2013). Two IAS, i.e. *Ailanthus altissima* and *Trachycarpus fortunei*, exhibited the highest C-scores. In general, among IAS we found a solid signal towards more competitive species, considering both the CSR ternary combination, and the dimension of each single axis. Indeed, above all growth forms, trees were the only one to show significant differences within the CSR space. For trees, it is likely that IAS are fast-growing species that can more rapidly fill empty gaps following clear-cuts,

while late-successional species have not been imported, except for a few exceptions (e.g. *Quercus rubra*). Guo et al. (2018) found that the naturalization incidence and extent of trees is not, or is only weakly, affected by their C-, S-, and R- scores. Differences with our findings could be due, once again, to the fact that we have considered IAS, i.e. the portion of naturalized species that are already well established in new environments. Indeed, the naturalization of trees may occur over longer periods of establishment, long generation time, relatively low proportions of resources invested in seed production (Grime, 1979), and the long time lag following introduction to new ranges (Kowarik, 1995; Pyšek et al., 2017). Shrubs also prevail in the S-C region of the triangle (Grime, 2001; Pierce et al., 2013). However, in this case we found robust patterns only considering each axis as independent. The highest C-scores were associated with climber IAS such as *Vitis vulpina* and *Parthenocissus quinquefolia* as well as to *Pueraria montana*; the latter is a clonal species, which highlights that high clonality can correspond to greater invasive capacity (Song et al., 2013; Roioloa et al., 2016). In our dataset, the shrubs with the highest R- score were native species, i.e. *Thymus vulgaris* and *Myricaria germanica* (Fig. 1).

With regard to herbaceous growth forms, short-lived IAS showed high C-scores compared to natives according to Guo et al. (2018). Accordingly, short-lived herbs do not exhibit extensive ruderalism, probably because they are successfully invaders only under conditions of relatively low disturbance, while under continuous disturbance, the seed production of ruderal species does not compensate for the mortality rate, and they eventually fail to establish (Grime, 1979; 1988). Regarding long-lived herbs, it must be considered that in our dataset IAS represent only 3.7% of the total (Table 1), which may have affected outcomes; anyway, invasive alien long-lived herbs are homogenously distributed in the CSR space (Fig. 1), without forming clusters, similarly to natives. However, competitive and large-leaved invasive herbs capable of forming monospecific stands in productive habitats were classified towards the C-selected corner, for example *Phytolacca americana*, *Reynoutria* x *bohemica*, or *Helianthus tuberosus* (Pierce et al., 2013). Aquatic plants displayed clear preferences towards ruderal strategies, for both IAS and native species (Fig. 1), confirming previous observations (Pierce et al., 2012; 2013). Aquatic species were either small, fast growing and with extremely acquisitive leaves (highly R-selected) or CS to C-selected species with large, broad leaves, such as water lilies, in agreement with previous conclusions (Pierce et al., 2012). Among IAS, *Nelumbo nucifera* displayed the highest C-scores, and in the CSR spectrum clustered together with other native *Nymphaeiden* (Pierce et al., 2012). Several traits of this species may form part of the C-selected syndrome (Bornette et al., 2008), including moderate relative growth rates, limited vegetative dispersal and seeds that sink immediately. Many aquatic species are R selected in the extreme, as they mainly rely on rapid generation to face disturbance, indeed most hydrophytes are typical of disturbed habitats, as they colonize areas where seasonal flooding washes away the existing vegetation (Bornette et al., 2008). No hydrophyte species in our study exhibited selection toward the extreme of conservative S- corner, also confirming that hydrophyte IAS may not include stress tolerators *sensu* Grime (1979) (Kautsky, 1988; Pierce et al., 2012). Previous observations of functional traits of hydrophytes (Lukács et al., 2017) found that traits of IAS are linked to competitive ability ('soft leaves faster'). However, we cannot confirm such differences because the functional traits of alien aquatic plants depend strongly on their growth-form (see Lukács et al., 2017).

Conclusions

In the ternary space determined by CSR classification, IAS and native species cover almost the same region, indicating that IAS can occupy the same niches and have the same requirements of native species. This supports the idea that a complex of factors, which act in conjunction with the carbon accumulation strategies, mediates the mechanisms that regulate the invasion of empty gaps in vegetation communities. Several authors stressed that the spread of IAS is linked to the pivotal contribution of: 1) the phylogenetic similarity between alien and native species (Ordonez, 2014; Loiola et al., 2018); 2) the capability of habitat features to drive IAS establishment (Carboni et al., 2015); 3) habitat invasibility (Richardson & Pyšek, 2006; Leishman et al., 2010; Rejmánek et al., 2005b), 4) as well as the role of biogeographical context (Pyšek & Richardson, 2006). Analysing each axis of CSR independently, we found broad evidence that IAS are mainly true competitors, suggesting that traits that can describe the invasiveness ability of alien plants at the regional scale are those underlined by the C-selection strategy.

Further studies are necessary to implement our findings; in particular, we need to understand differences among distinct environments and habitats according to Grime's theory and the ecology of invasive plants (Rejmánek et al., 2005a; van Kleunen et al., 2018). Global changes and the flora globalization will promote the establishment of competitive alien functional types in Southern Europe (Walther et al., 2002; Ciappetta et al., 2016; Najberek et al., 2017; Dalle Fratte et al., 2018). In this context, CSR theory can be a viable tool for the risk assessment of IAS (Vicente et al., 2013), implementing the current approaches of prioritization methods and horizon scanning (Carboneras et al., 2018), and the development of non-invasive ideotypes of crops and horticultural plants (Anderson et al., 2006; van Kleunen et al., 2018a; Guo et al., 2019).

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562 **Table 1:** Summary of the number (n) and percentage of invasive alien and native species within all
563 the dataset and each growth form.

	n	%
ALL SPECIES	**1039**	**100.0**
invasive	110	10.6
native	929	89.4
TREES	**59**	**100.0**
invasive	17	28.8
native	42	71.2
SHRUBS	**94**	**100.0**
invasive	16	17.0
native	78	83.0
SHORT-LIVED HERBS	**224**	**100.0**
invasive	46	20.5
native	178	79.5
LONG-LIVED HERBS	**601**	**100.0**
invasive	22	3.7
native	579	96.3
HYDROPHYTES	**61**	**100.0**
invasive	9	14.8
native	52	85.2

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Table 2: Results of the phylogenetic multivariate analysis of variance (MANOVA) among invasive alien and native species CSR compositional data within all species and each growth form, indicating Wilk's statistics, F-values and phylogenetic p-values. Coefficients in bold are statistically significant ($p<0.05$).

	Wilks	F	p-value
all species	0.998	0.92	0.60
trees	**0.862**	**4.50**	**0.02**
shrubs	0.960	1.87	0.25
short-lived herbs	0.978	2.46	0.27
long-lived herbs	0.999	0.37	0.85
hydrophytes	0.935	2.01	0.38

Table 3: Results of the phylogenetic univariate analysis of variance (MANOVA) among invasive alien and native species C-, S-, and R- scores, within all species and each growth form, indicating F-values and phylogenetic p-values. Coefficients in bold are statistically significant ($p<0.05$).

	C		S		R	
	F	p-value	F	p-value	F	p-value
all species	**9.09**	**0.03**	1.76	0.27	1.17	0.47
trees	**4.91**	**0.05**	1.68	0.29	0.88	0.50
shrubs	**18.70**	**0.01**	**7.68**	**0.02**	0.02	0.89
short-lived herbs	**6.08**	**0.05**	0.00	0.98	5.01	0.15
long-lived herbs	0.26	0.66	0.01	0.96	0.38	0.69
hydrophytes	0.25	0.82	0.00	0.97	0.14	0.83

Fig. 1: Invasive alien (red dots) and native (blue dots) species within the CSR strategies triangle. Legend: a) all species, b) trees, c) shrubs, d) short-lived herbs, e) long-lived herbs, f) hydrophytes. Star indicates statistically significant difference between invasive and native species ($p<0.05$).

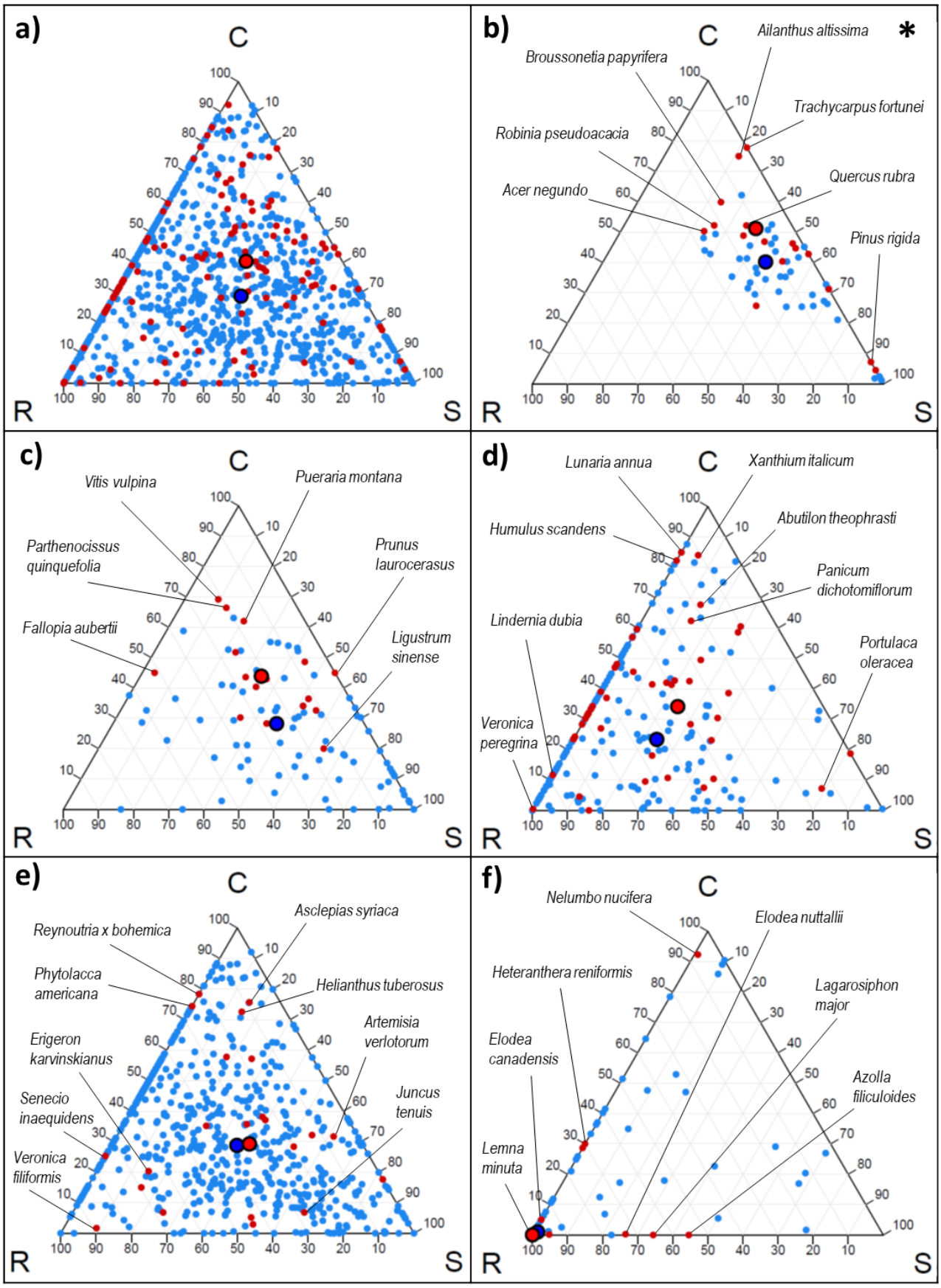
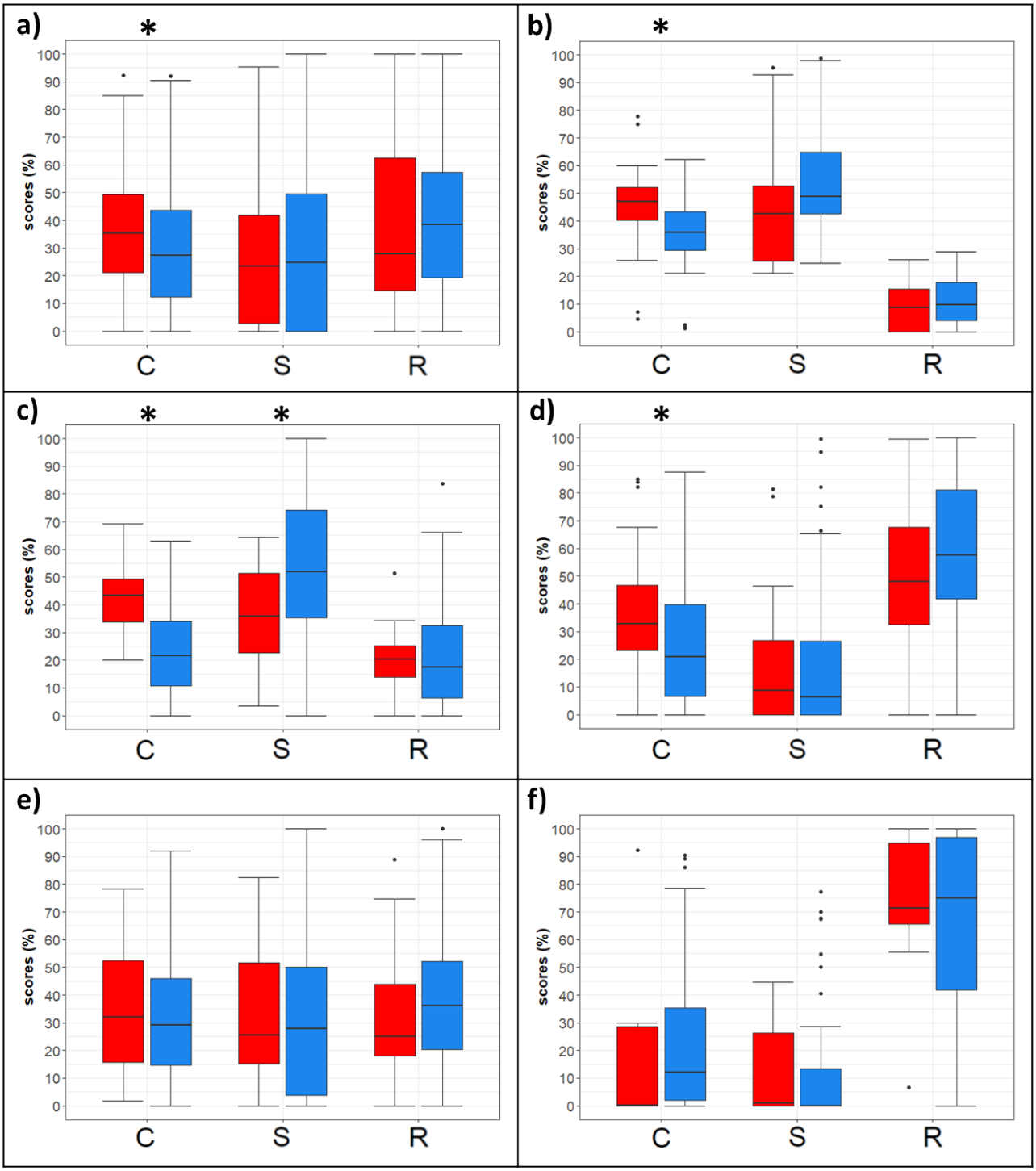


Fig. 2: Boxplots of C-, S-, R- strategy scores of invasive alien (red) and native (blue) species displaying the median (line in the middle of the boxes), the interquartile range (boxes), ± 1.5 times the interquartile range (whiskers) and outliers (circles) for all species and each group form. Legend: a) all species, b) trees, c) shrubs, d) short-lived herbs, e) long-lived herbs, f) hydrophytes. Star indicates statistically significant difference between invasive and native species ($p<0.05$).



588 **Appendix A:** CSR compositional mean (mean ± standard deviations) within all species and the
589 analysed growth forms.

		C:S:R ± sd
ALL SPECIES	**invasive**	40.4:32.0:27.5 ± 25.1
	native	28.9:36.3:34.8 ± 25.8
TREES	**invasive**	51.2:38.0:10.8 ± 24.7
	native	40.2:46.3:13.5 ± 22.5
SHRUBS	**invasive**	43.9:34.6:21.6 ± 17.4
	native	28.2:46.7:25.0 ± 26.0
SHORT-LIVED HERBS	**invasive**	34.2:24.3:41.5 ± 25.6
	native	23.4:23.8:52.9 ± 29.2
LONG-LIVED HERBS	**invasive**	40.4:32.0:27.5 ± 23.9
	native	29.0:36.6:34.4 ± 25.1
HYDROPHYTES	**invasive**	0.1:0.0:99.9 ± 36.7
	native	0.3:0.0:99.7 ± 35.6

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Appendix B: C-, S-, and R-scores (mean ± standard deviations) within all species and the analysed growth forms.

		C (%) ± sd	S (%) ± sd	R (%) ± sd
ALL SPECIES	**invasive**	36.3 ± 21.4	26.4 ± 27.8	37.3 ± 26.3
	native	29.8 ± 21.6	30.0 ± 27.4	40.2 ± 26.5
TREES	**invasive**	44.5 ± 19.4	46.4 ± 22.8	9.1 ± 9.0
	native	34.6 ± 13.7	53.9 ± 19.1	11.5 ± 8.7
SHRUBS	**invasive**	43.5 ± 13.8	35.9 ± 18.0	20.6 ± 11.9
	native	23.9 ± 17.0	54.8 ± 26.0	21.3 ± 19.4
SHORT-LIVED HERBS	**invasive**	35.5 ± 21.5	15.9 ± 20.0	48.6 ± 24.2
	native	26.3 ± 22.8	15.7 ± 20.8	58.0 ± 25.5
LONG-LIVED HERBS	**invasive**	34.4 ± 25.1	31.6 ± 23.3	34.0 ± 24.7
	native	32.0 ± 21.2	31.0 ± 27.2	37.0 ± 22.1
HYDROPHYTES	**invasive**	17.4 ± 30.7	12.4 ± 17.8	70.3 ± 28.3
	native	22.1 ± 25.3	11.9 ± 21.2	65.9 ± 32.9